

Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils

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The relative contribution of different types of litter to the maintenance of soil organic matter and nitrogen levels cannot be determined from standard litter bag disappearance studies. By coupling measurements of weight loss with nitrogen dynamics and presenting results in a new format, estimates of both state of decay and percentage of material eventually transferred to lower soil horizons can be obtained.

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La contribution relative de différents types de litière à la conservation de la matière organique du sol et au maintien du niveau d'azote dans le sol ne peut être déterminée par des études standards de disparition dans des sacs de litière. En associant la dynamique de l'azote à des mesures de perte en poids et en présentant les résultats d'une nouvelle façon, on peut obtenir des estimés à la fois de l'état de décomposition et du pourcentage de matériel éventuellement transféré aux horizons inférieurs du sol.

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Introduction

The decomposition of plant litter materials is the primary mechanism by which organic matter and nutrients are returned to forest soils, and has recently received considerable attention. Decomposition or disappearance rates have been determined for a wide variety of litter types throughout the world and recent syntheses by Meentemeyer (1978) and Fogel and Cromack (1977) have begun to explain or predict these as a function of climate and substrate quality. Despite this work, no method has yet been offered for determining what portion of the decomposing material actually becomes incorporated into soil organic matter and what its nutrient content is at the time of incorporation. There is no method for determining when the material remaining in a litter bag would, if unconfined, become indistinguishable from the 021 horizon or, more importantly, when it would begin to function as a part of this horizon. Thus there is no way to judge the relative contribution of different types of litter to soil organic matter and nutrient stocks. For this we must know rates of litter input, rates of decomposition and accompanying nutrient dynamics, plus the point at which the remaining material changes from "litter" in the 01 horizon to soil organic matter in the 021. The importance of this

determination has been emphasized by a computer model of litter and forest floor dynamics which we have used to predict the effects of different management techniques on nitrogen availability (Aber *et al.* 1978). The model proved very sensitive to this "percentage transfer" parameter for which a number of assumptions had to be made. Viewed in another way, the relative contribution of different types of organic soil amendments (the agricultural equivalent of litter) to soil organics, and especially the nitrogen immobilization-mineralization characteristics of the material through time, remains a classic and unanswered problem. The purpose of this paper is to present a method for estimating this percentage transfer value for different litter types as well as for predicting the relative changes in weight and nitrogen content through time.

The method

In our work with the forest floor model we began seeking a method for predicting the changes in weight and nitrogen content through time and for expressing this in a single function to be used to estimate the percentage transfer parameter. Data from Gosz *et al.* (1973) were replotted on the axes shown in Fig. 1 which expresses the percentage of

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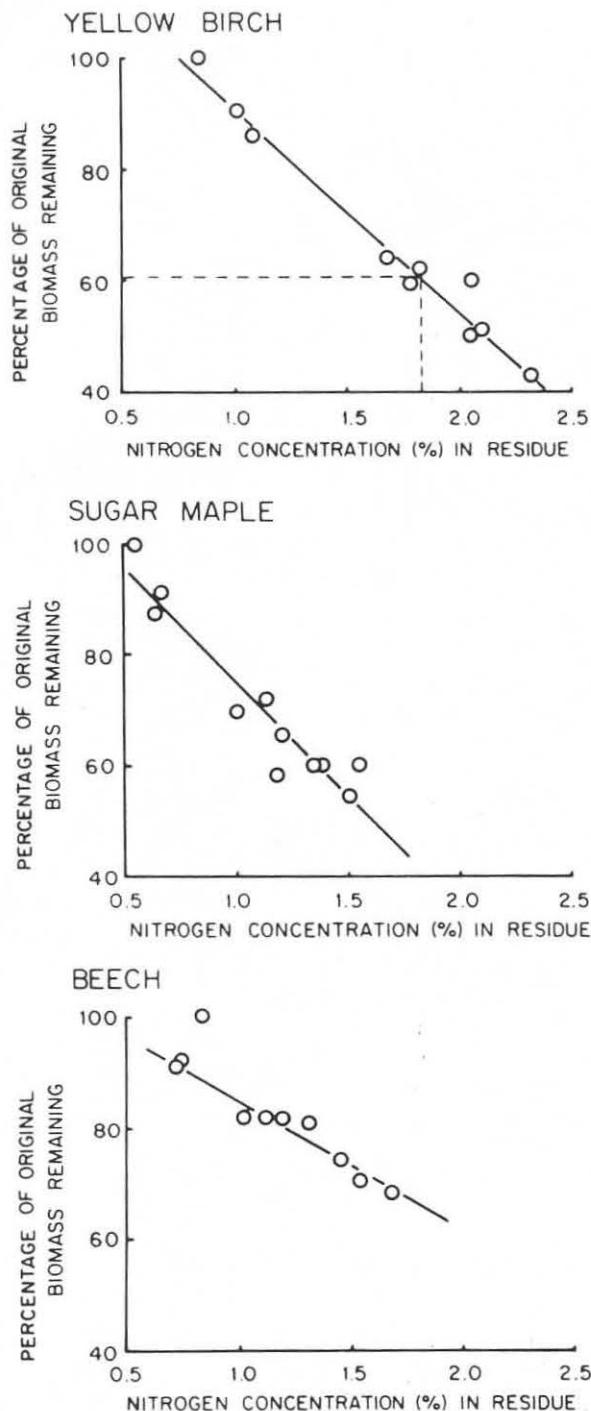


FIG. 1. Results of a leaf litter decomposition study by Gosz *et al.* (1973) replotted to express the percentage of original biomass remaining as a function of the nitrogen concentration in the residual material. Slopes and correlation coefficients for regressions are given in Table I (Nos. 1-3). The point where the dotted line intersects the X -axis of the yellow birch graph marks the

original biomass remaining as a function of the nitrogen concentration in the residual material. The results yield an inverse linear regression with a very high correlation coefficient for all three species of leaf litter (see Table I, Nos. 1-3, and Fig. 1). Linearity is also substantiated by analysis of residuals from the regression.

Since this relationship had not previously been reported we searched the literature for other studies for which both weight and nitrogen values are available. Table I summarizes the results of this survey and strongly substantiates the generality of the inverse linear relationship in cases where (1) physical removal of material from bags is minimized; (2) nitrogen is sufficiently low in concentration in the litter material to be limiting to microbes; and (3) a continuous external source of nitrogen is available. All of the field studies on nonmull soils (Nos. 1-26) (except those with a very high initial nitrogen concentration (e.g., No. 12)), all but one of the stream studies (Nos. 39-43), and those laboratory studies where litter was mixed with manure or provided with a constant nitrogen source (Nos. 55-61), exhibit this inverse linear relationship.

Those studies carried out on mull soils in the field exhibit a degree of noise, most probably due to the confusion of decomposition or actual mineralization of litter material in place by microbes and soil microfauna with disappearance which includes both decomposition and the physical removal of material by the macrofauna, especially earthworms, which are far more active in mull soils. On the axes of Fig. 1, this physical removal adds noise to the inverse linear function (poorer correlation) and generally increases the slope, indicating a larger weight loss per unit increase in nitrogen content. This could result from selective feeding by the macrofauna on the more palatable high-nitrogen material being constantly produced by microbial growth and activity.

Laboratory studies using no continuous external source of nitrogen (e.g., No. 62) will produce results which are better described by an exponential rather than a linear equation. Linearity on the axes of Fig. 1 and in the range of slopes and initial nitro-

switch from net immobilization to net mineralization which indicates the 61% transfer value for this type of material. The first point in the beech data was ignored as the initial decrease in both weight and nitrogen concentration was considered a leaching rather than a decomposition phenomenon (Nykvist 1963). Only one other set of data used in Table I (No. 39) exhibited a distinct early leaching period which was deleted from the regression analysis.

TABLE I. Data from studies in the literature which measured changes in both biomass and nitrogen content in decomposing tissues were used to determine the slope and correlation coefficient for a linear regression between percentage original weight remaining and nitrogen concentration in the residual material

No. Genus	No. of points	Original concn. of N, %	Slope	Correlation coefficient	Source
Leaves in forest (nonmull soil)					
1. <i>Acer</i>	10	0.56	-35.5	-0.92	Gosz et al. (1973)
2. <i>Fagus</i>	10	0.82	-22.7	-0.96	Gosz et al. (1973)
3. <i>Betula</i>	10	0.85	-36.6	-0.98	Gosz et al. (1973)
4. <i>Quercus</i>	7	0.73	-45.5	-0.96	Bocock et al. (1960)
5. <i>Fraxinus</i>	7	1.48	-59.3	-0.96	Gilbert and Bocock (1960)
6. <i>Pseudotsuga</i>	8	0.82	-49.6	-0.92	R. Fogel and K. Cromack (personal communication)
7. <i>Quercus</i>	2	0.92	-41.2	*	Bocock (1963)
8. <i>Fraxinus</i>	7	1.55	-87.3	-0.95	Bocock (1963)
9. <i>Quercus</i>	5	0.77	-42.6	-0.96	Bocock (1964)
10. <i>Corylus</i>	4	1.39	-50.5	-0.99	Bocock (1964)
11. <i>Alnus</i>	4	3.06	-76.1	-0.73	Bocock (1964)
12. <i>Acer</i>	4	2.52	**	*	Bocock (1964)
13. <i>Quercus</i>	2	0.77	-37.8	*	Bocock (1964)
14. <i>Quercus</i>	2	0.79	-28.8	*	Bocock (1964)
15. <i>Rhododendron</i>	2	0.40	-111.5	*	Bocock (1964)
16. <i>Prunus</i>	4	1.12	-100.4	-0.96	Bocock (1964)
17. <i>Fagus</i>	2	1.17	-37.3	*	Bocock (1964)
18. <i>Castanea</i>	5	0.77	-41.0	-0.86	Anderson (1978)
19. <i>Fagus</i>	5	0.56	-36.5	-0.96	Anderson (1978)
20. <i>Quercus</i>	10	1.04	-34.9	-0.96	Strojan (1973)
21. <i>Sassafrass</i>	10	1.42	-28.1	-0.94	Strojan (1973)
22. <i>Prunus</i>	5	1.15	-21.3	-0.95	Melillo et al. (unpublished)
23. <i>Acer</i>	4	1.01	-38.9	-0.94	Melillo et al. (unpublished)
24. <i>Betula</i>	3	0.92	-29.7	-0.93	Melillo et al. (unpublished)
25. <i>Fraxinus</i>	5	1.01	-32.1	-0.89	Melillo et al. (unpublished)
26. <i>Fagus</i>	5	0.90	-11.5	-0.87	Melillo et al. (unpublished)
Leaves in forest (mull soil)					
27. <i>Quercus</i>	3	0.73	-110.3	-0.97	Bocock et al. (1960); Gilbert and Bocock (1960)
28. <i>Fraxinus</i>	7	1.48	**	*	Bocock et al. (1960); Gilbert and Bocock (1960)
29. <i>Fraxinus</i>	4	1.55	**	*	Bocock (1964)
30. <i>Quercus</i>	4	0.77	-87.3	-0.97	Bocock (1964)
31. <i>Corylus</i>	4	1.39	-161.1	-0.97	Bocock (1964)
32. <i>Alnus</i>	4	3.06	**	*	Bocock (1964)
33. <i>Acer</i>	3	2.52	-37.5	-0.81	Bocock (1964)
34. <i>Quercus</i>	2	0.77	-115.6	*	Bocock (1964)
35. <i>Quercus</i>	2	0.79	-72.8	*	Bocock (1964)
36. <i>Rhododendron</i>	2	0.40	-91.9	*	Bocock (1964)
37. <i>Prunus</i>	4	1.12	**	*	Bocock (1964)
38. <i>Fagus</i>	2	1.17	-37.2	*	Bocock (1964)
Leaves in stream					
39. <i>Carya</i>	12	1.50	-45.7	-0.90	Suberkropp et al. (1976)
40. <i>Quercus</i>	11	0.70	-52.1	-0.98	Suberkropp et al. (1976)
41. <i>Salix</i>	8	1.79	**	*	Mathews and Kowalcowski (1963)
42. <i>Platanus</i>	8	1.43	-74.3	-0.91	Mathews and Kowalcowski (1963)
43. <i>Quercus</i>	7	1.28	-52.9	-0.85	Mathews and Kowalcowski (1963)
Wood					
44. <i>Quercus</i>	3	—	-77.7	-0.97	Allison and Murphy (1962); Allison et al. (1963)
45. <i>Quercus</i>	3	—	-41.9	-0.99	Allison and Murphy (1962); Allison et al. (1963)
46. <i>Quercus</i>	3	—	-46.7	-0.99	Allison and Murphy (1962); Allison et al. (1963)
47. <i>Quercus</i>	3	—	-39.2	-0.98	Allison and Murphy (1962); Allison et al. (1963)

TABLE 1. (Concluded)

No. Genus	No. of points	Original concn. of N, %	Slope	Correlation coefficient	Source
48. <i>Carya</i>	3	—	-46.3	-0.99	Allison and Murphy (1962); Allison et al. (1963)
Wood					
49. <i>Liquidambar</i>	3	—	-41.4	-0.89	Allison and Murphy (1962); Allison et al. (1963)
50. <i>Liriodendron</i>	3	—	-80.8	-0.82	Allison and Murphy (1962); Allison et al. (1963)
51. <i>Castanea</i>	3	—	-24.6	-0.99	Allison and Murphy (1962); Allison et al. (1963)
52. <i>Juglans</i>	3	—	-74.6	-0.98	Allison and Murphy (1962); Allison et al. (1963)
53. <i>Pseudotsuga</i>	5	0.075	-350.0	-0.89	Franklin (personal communication)
54. <i>Tsuga</i>	7	0.065	-427.4	-0.97	Grier (1978)
Laboratory studies					
55. Flax	5	0.51	-28.5	-0.97	Richards and Norman (1931)
56. Flax (retted)	5	0.21	-34.9	-0.92	Richards and Norman (1931)
57. Flax fibre	5	0.55	-28.4	-0.87	Richards and Norman (1931)
58. Willow peelings	5	1.58	-8.3	-0.83	Richards and Norman (1931)
59. Willow peelings	5	1.58	-25.6	-0.99	Richards and Norman (1931)
60. Oat straw	5	0.30	-20.4	-0.86	Richards and Norman (1931)
61. Oat straw	6	1.82	-27.0	-0.93	Peevey and Norman (1948)
62. Conifer litter	6	0.79	-70.3	-0.86	Iverson and Sowden (1959)
63. Hardwood litter	6	1.01	-52.4	-0.97	Iverson and Sowden (1959)

*Studies with two data points for which this statistic cannot be computed.

**No statistically significant regression for this set of data.

gen concentrations listed in Table 1 requires an initial increase in the absolute amount of nitrogen (as well as in its concentration) which represents immobilization of nitrogen from the surrounding environment by decomposers. In closed-system laboratory experiments, including those which provide an initial input of nitrogen and no additional inputs, this external source is lacking, total nitrogen content remains nearly constant, and the results appear as an exponential decay curve on the axes of Fig. 1. Interestingly, the results from one study on the decomposition of whole logs (No. 53) also fit an exponential equation better than a linear one, perhaps indicating an isolation from sources of immobilizable nitrogen due to its position above the forest floor and hence relatively little direct contact with areas of active nitrogen mineralization. However, data on whole log decomposition by Grier (No. 54) and on sawdust by Allison et al. (Nos. 44–52) do exhibit linearity indicating initial immobilization. Much more information on the decomposition of whole logs and other woody substrates is needed.

Using the inverse linear relationship to predict percentage transfer

Having described both the organic matter and nitrogen dynamics of decomposing litter in a single linear function, it is now possible to determine the

amount of each transferred from litter to soil compartments (or horizons) by determining the point along the line at which the transfer is made. This requires a strict definition of the terms litter and soil or of the difference between the 01 and 021 horizons. This has traditionally been accomplished observationally by more or less arbitrary criteria which can be interpreted differently by different workers. We propose to distinguish between them on the basis of their role in the nitrogen availability of the system. Thus "litter" becomes any material which exhibits net nitrogen immobilization, and "soil" any material which exhibits net mineralization. This definition is both more functional (and therefore more meaningful in terms of overall system function) and less arbitrary.

It is interesting that the birch leaves in Fig. 1, the only ones which decomposed fast enough to switch from net immobilization to net mineralization in the course of Gosz's study, did so at exactly the nitrogen concentration of the 021 layer as distinguished visually (Gosz et al. 1976, 1.83%). Gosz et al. (1976) also observed that, at this time (June of the year following leaf fall), birch leaves could no longer be distinguished in the 01 layer. Thus there is initial circumstantial evidence that, in nonnull soils, the functional and observational definitions may coincide. This might be explained in part by the importance of nitrogen availability to root growth (Saf-

ford 1974) which would cause root penetration into decomposing leaves to begin when net mineralization occurred and not before. This root growth would help bind the weakened material into the unit recognized as the 021 horizon. Similar patterns may not occur in mull soils where litter and soil, by the functional definition, are thoroughly mixed creating variation from immobilization to mineralization on a microscale rather than on a macroscale or horizontal scale.

Having defined the inverse linear relationship and the point of change from immobilization to mineralization it is a simple matter to determine the percentage of original material transferred to the 021 by reading off the *Y*-axis in Fig. 1. For the yellow birch example, this value would be 61%. We might expect very different transfer percentages for litter materials of different types. In a system for which all of the transfer percentages have been determined, matching these values with annual input values and decomposition rates would provide a precise determination of the relative contribution of each type of material to soil organic matter. It would also estimate the timing and amount of nitrogen released from any material, a facility which might be of value in green manuring or composting applications.

Other applications of this technique

This type of analysis suggests methods for answering other difficult and important questions regarding litter decomposition and also raises some intriguing new ones. One simple application would be to use the type of relationship derived in Fig. 1 (with different slopes and intercepts for each litter type) to predict the percentage of original material remaining at any point in time by its nitrogen concentration.

A more interesting question is the relationship between this inverse linear function and the microbial dynamics which must underlie it. For example, assuming that the material in the litter bag contains only microbes with a certain percentage of nitrogen in their protoplasm and remaining litter substrate at the original concentration, meaning that all of the change in nitrogen concentration of the residue is due to increased microbial biomass, then this biomass can be calculated directly from the regressions in Fig. 1 (see Fig. 2). In reality, this analysis will be clouded by the accumulation of secondary compounds with different (mainly higher) nitrogen concentrations. Still, the possibility of calculating microbial biomass by difference after these corrections have been made is one which should warrant further attention.

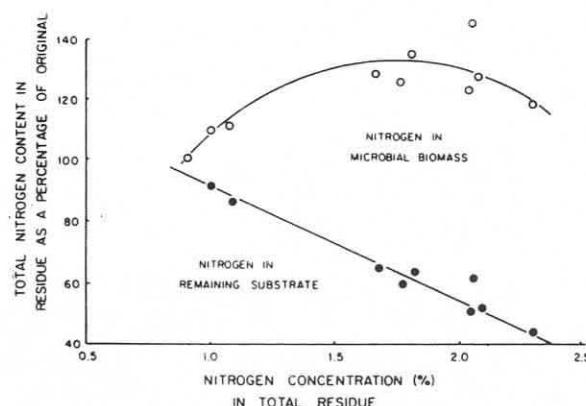


FIG. 2. Separation of nitrogen in residual material within litter bags into microbial biomass and remaining undecomposed substrate using yellow birch data (Fig. 1A). Lower line represents nitrogen in substrate which is described by the same function as weight loss assuming that the nitrogen concentration in this material does not change with time (equation is $Y = 128.1 - 36.6X$ where X is the nitrogen concentration (%) in the combined microbe-substrate residue). The upper line represents total nitrogen in the residue (equation is $(128.1 - 36.6X)X/0.85$, where 0.85 is the original nitrogen concentration of the fresh birch litter). The difference between the two lines for any value of X represents the nitrogen content of microbial biomass at that point in the decomposition process. See text for assumptions and qualifications. The pattern of initial net immobilization (increase in total nitrogen content) followed by net mineralization beginning at a nitrogen concentration of 1.83% can also be seen in this figure.

An additional question posed by the analysis is, What determines the slope of the linear relationship? From the above, changes in weight indicate respiratory loss of organic carbon while changes in nitrogen content indicate changes in the quantity of microbial protoplasm. Thus the axes represent carbon respired per net unit nitrogen (and hence by the stoichiometry of microbial protoplasm, carbon) fixed, or a measure of the efficiency of substrate utilization (Gosselink and Kirby 1974). This efficiency may be affected by substrate quality, temperature, particle size, or position with respect to available nitrogen, which may in turn affect site organic matter and nitrogen budgets, feeding back to litter quality or other soil properties.

A final question raised is, What is the end point for the process described in Fig. 1? It cannot proceed beyond the projected intersection with the *X*-axis and it may not even approach this axis. It is interesting that, at least for yellow birch, the linearity holds well beyond the projected switch from litter to soil, indicating that the process described by this relationship continues into the 021 horizon. Litter decomposition studies generally do not last the 2–3 years required to examine the validity of this linear relationship to the termination of the decom-

position process. We can, however, conjecture that it will continue as described in Fig. 1 until the exhaustion of readily decomposable substrate leaves only a residue of recalcitrant secondary products. This point might represent each type of litter's contribution to long term organic matter storage in the humic compounds of the 022 and other horizons.

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